RIPARIAN INFLUENCE ON EASTERN FOREST SONGBIRDS AT THEIR WESTERN RANGE LIMIT

By

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Abstract:
The Cross Timbers is a transitional landscape between the eastern temperate deciduous forests and the grasslands of the Central Great Plains. Here many eastern forest birds reach the western edge of their breeding ranges. In a water-limited environment, water resources are likely important in determining species distributions. Differences between riparian and upland forests may influence bird community composition and species distributions in this sub-humid to semi-arid climate. We conducted paired upland-riparian surveys for a total of 178 point counts across central Oklahoma. Ordination techniques were used to investigate how riparian and upland forest type influence eastern songbird distribution and how bird species distributions were organized by forest cover and surface water patterns along a precipitation gradient. Most eastern species, including the Kentucky Warbler and Red-eyed Vireo, were more common in riparian than upland forests. Riparian forests were more similar to eastern oak-hickory forests in structure and composition and had higher food availability for foliage gleaning insectivorous species. We also found that most eastern forest species were limited to regions of higher precipitation or to areas of higher flow accumulation, whereas generalist species showed no strong response to precipitation or surface water flow gradients. Flow accumulation was a better predictor of species occurrences in xeric Cross Timbers forests than in mesic oak-hickory stands for several eastern forest species typically found in wetter climates. With projected increases in temperature and declines in precipitation, it is important to identify species sensitive to water resource gradients and predict how changes will affect species distributions.

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CHAPTER I

RIPARIAN INFLUENCE ON EASTERN FOREST SONGBIRDS IN OKLAHOMA'S CROSS TIMBERS

INTRODUCTION

Species' distributions can be limited by multiple biotic and abiotic influences (Lomolino et al. 2006). Species at their range limits are under increased environmental stress at the threshold of their ecological niche (Holt and Keitt 2005). For conservation planning and forecasting species responses to climate change, it is important to understand how biotic and abiotic factors mechanistically limit species ranges (Gaston 2003). Plants and bird species are better able to track environmental conditions and stay at equilibrium with their climatic niche compared to other taxa such as reptiles and amphibians (Araujo et al. 2005). In the Cross Timbers of central Oklahoma, precipitation and forest cover limit the extent of many eastern forest songbirds breeding ranges. In this relatively dry climate, we are interested in how upland-riparian forest gradients organize bird communities and the mechanisms that explain patterns of eastern forest bird distributions at their range limit.

Riparian zones embedded within upland environmentas can result in corridors of moister

Soils, higher plant species diversity, and different light and temperature conditions compared to upland environments (Naiman et al. 1993). Because of this habitat complexity, riparian environments are rich in biodiversity (Naiman et al. 1993). The majority of studies comparing upland and riparian bird communities provide evidence of this. Bird species richness, diversity, abundance, and density measures were found to be higher in riparian environments across many landscapes, including desert riparian woodlands along the Lower Colorado River (Szaro and Jakle 1985), in arid western ecosystems of northern Colorado (Knopf 1985), mixed conifer–deciduous forests in the central Appalachian Mountains (Gates and Giffen 1991), northern hardwood forests of Michigan (Bub et al. 2004), and boreal forests of northeastern Canada (LaRue et al. 1995). However, these results are not universal. One study in the boreal forest of Canada found no difference in community diversity or abundance measures between upland and riparian environments (Whitaker and Montevecchi 1997), and another study in the mixed deciduous–coniferous forests of the Pacific Northwest found species diversity, richness and total bird abundance to be higher in upland forests (McGarigal and McComb 1992).

In addition to community measures of diversity and abundance, specialists and life history guilds respond to environmental gradients (O'Connell et al. 1998, Croonquist and Brooks 1991). Studies comparing upland and riparian communities identified bird species and guilds with greater affinity for riparian forests. Along the Lower Colorado River, migratory birds required riparian woodland vegetation for suitable breeding habitat over adjacent desert wash and desert scrub environments (Szaro and Jakle 1985). In the mixed forests of the Appalachian Mountains, most neotropical migrant species were associated with bottomland forests, and many of these species were forest–interior or area–sensitive species (Gates and Giffin 1991). In the boreal forests, the abundance of species in the shrub–foraging guild was higher in riparian stands (LaRue et al. 1995). In the northern hardwood forests of Michigan, foliage–gleaning birds were more abundant in riparian forests (Bub et al. 2004). The responses of bird communities, guilds,

and species are region–specific and related to the life–history strategies of individuals (James and Harner 1982).

In the US Great Plains, a prevailing longitudinal gradient of precipitation marks the broad ecotone between predominantly forested ecoregions of eastern North America and grasslands that grade from tallgrass to shortgrass prairie approaching the Rocky Mountains. Several eastern forest songbirds reach the western edge of their breeding range in the Cross Timbers ecoregion of central Oklahoma (Reinking 2004), where mesic deciduous forests transition into xeric woodland and tallgrass prairie (Woods et al. 2005). Populations of species at the margins of their climatic niche are thought to be more stressed than those closer to the center of their distribution (Thuiller et al. 2005). Subtle differences in deciduous vegetation between upland and riparian environments could be important for organizing forest bird communities in this transitional ecoregion. The microclimate, vegetation composition, and vegetation structure of riparian forests may provide favorable habitat for eastern birds typically found in areas with higher precipitation (Haas 2002, Baum et al. 2004, Woinarski et al. 2000).

The objectives of this study were to (1) determine the effects of upland and riparian forest type on bird community composition and the distribution of eastern forest songbirds and (2) investigate the mechanisms explaining the relationship between bird community composition and forest types in terms of vegetation structure, tree species composition, food availability, and microclimate.

METHODS

Study Area.— Our study was conducted on a mix of private and public lands across a five–county area in the Cross Timbers ecoregion of central Oklahoma. Average annual precipitation in this forest ecotone ranges from 90–115 cm and average monthly temperatures in May through August range 20–28°C with maximum temperatures ranging 25–36°C (PRISM

Climate Group, 2014). This Cross Timbers forms a mosaic of oak forests, savannas, and tallgrass prairie between the eastern deciduous forests and the grasslands of the Central Great Plains (Woods et al. 2005). Forest patches in this region are dominated by post (*Quercus stellata*) and blackjack (*Quercus marilandica*) oaks in uplands and a mix of oaks, elms (*Ulmus spp.*), bitternut hickory (*Carya cordiformis*), cottonwood (*Populus deltoids*), eastern redcedar (*Juniperus virginiana*), and other species in riparian zones (Hoagland 1998).

Prevailing vegetation structure and composition in the Cross Timbers are largely influenced by soil type and land use history, especially the frequency of fire (Hoagland 2000, DeSantis et al. 2011). Regeneration of both post and blackjack oak is largely through stump sprouting stimulated by fire. In contrast, eastern redcedar is fire intolerant. Widespread fire suppression in the 20th and 21st centuries has promoted an increase in basal area and tree density of post oak, an increase in mesophytic tree species such as elms and red mulberry, and encroachment of eastern redcedar as a mid–story and canopy tree in upland oak patches (DeSantis et al. 2010, Van Els et al. 2010).

Bird Surveys.— Bird surveys took place in May and June of 2013—2014. We conducted 8–minute, 100m–radius point counts (Ralph et al. 1993). One site included two riparian point counts paired with two adjacent upland point counts (Figure 1.). We surveyed 45 sites twice per breeding season with 90 riparian and 88 upland point counts, using a minimum distance of 50m between each pair of points.

Vegetation structure and composition. – Tree species composition and vegetation structure were characterized at each point count. Within a 10m radius at the center of each point count tree species and diameter at breast height (dbh) of all trees >2.54 cm dbh were measured with calipers and recorded. We characterized vegetation structure at three 5m radius plots for every point count. In riparian sites, one structure plot was done at the center of each point count,

one 30m from plot center along the creek bed, and one oriented 120° and 30m from the center plot (Figure 2.). In upland sites, one structure plot was at the center of the point count, a second was 30m uphill of the center, and a third at 120° and 30m from the other structure plots (Figure 2.). Visual estimations of percent cover of herbaceous plants, low woody vegetation at 0–2m height, and high woody vegetation at 2–5m height were recorded. Understory density of woody and herbaceous cover was measured using a 2m x 0.5m density board. Canopy height of the tallest tree was measured with a Haglof Vertex IV hypsometer to the tenth-of-a-meter. Canopy cover was measured from the center of each 5m radius plot in all four cardinal directions with a spherical densitometer.

Invertebrate sampling. – We collected invertebrates to quantify food availability for breeding birds. We sampled aerial insects, as well as invertebrates from the ground and foliage. In June and July of 2013, aerial insects were sampled using Malaise traps at one pair of upland-riparian point counts at 16 sites for a combined total of 54 sampling days. We had two Malaise traps, which were set up in pairs to sample an upland and riparian point count site over the same period and under the same weather conditions. Traps were set up at plot center for 2 to 4 days at a time and then rotated to another upland–riparian pair of point counts. Malaise traps passively sample flying insects, which intercept the tent mesh and instinctively crawl upwards into a collection head. Our traps were from BioQuip and are 7' tall, 4' wide on all sides, and have four central vanes of netting to intercept flying insects. We used Dichlorvos (Hot Shot® No–Pest®) as a killing agent in the dry head funnel trap (Hagar et al. 2012).

In June and July 2014 we quantified invertebrates from the ground and foliage. Ground invertebrates were collected from leaf litter and surface soils grab samples in a 25x25cm quadrat at the plot center of 73 point counts. We also collected invertebrates from branch clippings to quantify food availability for foliage–gleaning birds from 70 point counts (Johnson 2000). Branch clippings were collected from heights of 2–3m aboveground from the tree species closes

to plot center. Invertebrates sampled from the ground and foliage were collected on days with low wind and no rain. Samples were sorted in the field on a white sheet and invertebrates and leaves were kept for abundance and biomass measurements. Leaves were dried in an oven for one week at 60°C and invertebrates were dried for 24 hours at the same temperature before dry weights were measured for biomass (Hagar et al. 2012).

Microclimate. –We used an Ambient Weather WM-2 handheld weather meter to record air temperature, wind speed, and relative humidity at our point count locations. We collected weather data before each point count at approximately 1.5m above the ground.

Landscape characterization. –In addition to riparian and upland forest type, we calculated percent forested landscape within the 100m radius point count and within 1km of each site using 2006 National Land Cover Dataset in ArcMap. Forest cover included deciduous, coniferous, mixed, and woody wetlands classified at 30m resolution (Fry et al. 2011).

Data Analysis. –We were interested in the forest bird community's response to riparian–upland forest types as well as differences in the vegetation structure, composition, invertebrate availability, and microclimate between upland and riparian forest types. We also analyzed the partial explanatory power of forest type and percent forest cover at the point–count– and site–scales.

Bird Surveys.—For the community response analysis we used presence data at each point count, considering a species present if it was detected at least once during the two surveys. We removed grassland bird species from the analysis to focus on the response of forest and scrubland birds (Table 2.). Eastern forest songbirds were identified based on species accounts published in the Oklahoma Breeding Bird Atlas (Reinking, 2004). If the western edge a species' breeding range occurred in the Cross Timbers ecoregion, we considered that species to be eastern. The Atlas also served as a guide for identifying breeding status and habitat preferences of species

detected. We used partial Canonical Correspondence Analysis (pCCA) to test the hypothesis that riparian and upland forest bird communities differ in the Cross Timbers (Palmer 1993, Ter Braak 1986). Forest type, categorized as upland or riparian, was the only explanatory variable used to test its significance on variation in forest bird communities. Site was included as a covariate because of the blocked design of paired upland-riparian point counts. Analysis was conducted in CANOCO 5.03.

Vegetation structure and composition. – From the 10m radius plot, we calculated stand basal area, average tree dbh, tree species richness, and the relative basal area of upland and riparian–associated trees for every point count. Trees were classified *a priori* as upland, riparian, or generalists (Hoagland 1998) (Table 1.).

From the three 5m radius plots, we calculated canopy height, canopy density, herbaceous cover, low and high woody vegetation cover, and understory density by averaging these metrics for each point count.

We examined differences in riparian and upland forest structure and composition using a mixed ANOVA model (PROC MIXED in SAS 9.4). Forest type was the treatment analyzed, site was the blocking unit, and each pair of upland-riparian point counts were included as subsamples of a site. Weighted means were calculated using SAS LSMEANS and compared using Fisher's F-test (Smith and Goff 2014). Means were declared different if the null hypothesis was 0.05 or less. Microclimate conditions of upland and riparian forests, including maximum wind speed, average wind speed, percent relative humidity, and temperature were also compared using one–way ANOVA in program R (R Development Core Team, 2014).

Food availability.–To compare food availability between upland and riparian forest types, the abundance and biomass of invertebrate samples were compared using one–way ANOVA. For Malaise traps, we calculated the number and biomass of insects caught per day at

each site sampled. We then compared abundance and biomass capture rates by forests type. Sampling effort for ground–dwelling invertebrates was standardized by area surveyed, 25x25cm quadrats, so we compared raw abundance and biomass measurements between forest types. We counted the number of individuals and weighed the total biomass of invertebrates collected from branch clippings Leaves were collected, dried, and weighed from branch clippings to compare the biomass of foliage sampled between upland and riparian forests.

Landscape characterization.— In our final analysis, we tested the relative importance of forest type and forest cover on bird communities in a CCA. We used a stepwise forward selection with a Holm's method P–value correction

RESULTS

Forest bird communities.— We detected 55 bird species over the course of two breeding seasons and included 49 species in the community analysis after removing grassland species (Table 2.). Riparian and upland forest bird communities were significantly different according to the pCCA ($p=0.002$). The total adjusted variation explained by forest type alone was 8.2% and the eigenvalue of Axis 1 was 0.0900 (Figure 3.).

The American Goldfinch (AMGO), Painted Bunting (PABU), and Field Sparrow (FISP) were detected more frequently in upland forests. Several widely distributed forest generalists, including Carolina Wren (CARW), Yellow–billed Cuckoo (YBCU), and Blue–gray Gnatcatcher (BGGN) showed no preference for forest–type. Some eastern forest species such as Kentucky Warbler (KEWA), Northern Parula (NOPA), Acadian Flycatcher (ACFL), and Yellow–throated Vireo (YTVI) were found more frequently in riparian forests. Among the rarer species encountered and not included on the pCCA biplot, the Eastern Kingbird, Yellow–throated Warbler, Common Yellowthroat, Hooded Warbler, Yellow–breasted Chat, and Orchard Oriole

were only detected in riparian forests. The Bell's Vireo, Eastern Bluebird, Northern Mockingbird, Scarlet Tanager, and Eastern Whip–poor–will were only detected in upland forests.

Forest structure and composition.— Riparian and upland forest types differed in structure and tree species composition (Table 3). In terms of structure, riparian forests had taller, denser canopies compared to adjacent upland forests. In terms of tree species composition, riparian forests had a higher relative basal area of species associated with moist soils, such as American elm, sugarberry, bitternut hickory, and green ash (Table 3). Upland forests had a higher relative basal area of post oak and blackjack oak.

Food availability.— Total abundance of invertebrates on foliage was nearly two-times greater in riparian forests than in upland forests. There was no significant difference in invertebrate biomass from the foliage, in the abundance and biomass of aerial insects caught per day in Malaise traps, or in ground-dwelling invertebrates from quadrat samples (Table 4.).

Microclimate conditions.—No significant differences were found for temperature ($p = 0.539$), percent relative humidity ($p = 0.301$), or maximum wind speed ($p = 0.437$) and average wind speed ($p = 0.224$, One–Way ANOVA) between upland and riparian forests during morning bird surveys. Average morning survey conditions were 23.3°C, 75.4% relative humidity, and 1.4mph wind speed.

Landscape characterization.– Based on a stepwise forward selection process in a pCCA analysis, we found that forest type and forest cover at the point–count– and site– scale on bird communities accounted for 9.6% of adjusted explained variation in the Cross Timbers forest bird community (Figure 5., Table 5.). Forest type alone explained more than percent forest cover at the 100m and 1km scales, accounting for 76.4% of the total variation explained. Percent forest cover within 1km of each site accounted for 19.2% of total variation explained, while percent forest cover within 100m radius point counts accounted for 28.8%. When considering both the

marginal or conditional effects, forest type explained more variation than forest cover in bird community composition (Table 5.). The contribution of forest type and percent forested landscape within each 100m radius point count was significant using the Holm's correction in the forward selection process ($p = 0.008$), whereas percent forested land cover within 1km of each site was not significant ($p = 0.104$).

DISCUSSION

Upland and riparian forests in the Cross Timbers have distinct bird assemblages. Both forest types were dominated by deciduous trees, but differences in forest structure and composition between the two habitats provided distinct nesting and foraging opportunities for breeding birds. We found that several eastern forest songbirds responded to these subtle differences in vegetation, and riparian environments provide important habitat for these species occupying a relatively arid climate at the edge of their breeding distribution.

Across the forest–prairie ecotone the dramatic decline in precipitation changes forest structure and composition. Average annual rainfall at our sites in the Cross Timbers was approximately 100 cm per year, much lower than eastern deciduous forests (PRISM Climate Group 2014). Under the sub–humid to semi–arid conditions of the Cross Timbers, upland forests are a mixture of woodlands, savannas, and scrub intermixed with grasslands. By comparison, just east of the Cross Timbers average annual rainfall in the Ozark Highlands was 120 cm per year (PRISM Climate Group 2014). In the Ozark Highlands, forest cover increases and becomes more continuous across the landscape (Rice and Penfound 1959). These forests also have higher tree species diversity, with black hickory (*Carya texana*), mockernut hickory (*C. tomentosa*), black oak (*Quercus velutina*), shumard oak (*Q. shumardii*), white oak (*Q. alba*), winged elm (*Ulmus alata*), and sugar maple *(Acer saccharum*) emerging as dominants. Riparian forests in the Cross Timbers had taller, denser canopies, and higher tree species diversity, creating habitat more

similar in structure and composition to the eastern deciduous forests. We found that several eastern species at the western extent of their range took advantage of the microhabitat conditions available in Cross Timbers riparian forests. The Louisiana Waterthrush, Prothonotary Warbler, Yellow–throated Vireo, Acadian Flycatcher, Kentucky Warbler, Northern Parula, White–eyed Vireo, and Red–eyed Vireo were all found more frequently in riparian forests compared to adjacent uplands. Similar patterns of bird species biogeography were found in Australia's savanna ecosystems; riparian environments enable species to extend their range into more arid climates (Woinarski et al. 2000).

Upland–riparian associations seem to be region–specific for some species. The Red–eyed Vireo and Yellow–throated Vireo were associated with upland forests further east in areas such as the oak–hickory forests of Arkansas (Smith 1977), the mixed forests of the Appalachian Mountains (Gates and Giffen 1991), Arkansas forests (Wakeley and Roberts 1996), the northern hardwood forests of Michigan (Bub et al. 2004), or in the boreal forests of Canada (LaRue et al. 1995). However, these species were associated with riparian environments in the Cross Timbers savanna. Acadian Flycatcher and Northern Parula are associated with riparian forests across their breeding extent, including in the Cross Timbers, in the oak–hickory forests of Arkansas (Smith 1977), mature deciduous forests in Ohio (Bakermans and Rodewald 2006), the mixed forests of the Appalachian Mountains (Gates and Giffen 1991), the northern hardwood forests of Michigan (Bub et al. 2004), and boreal balsam fir forests of Canada (LaRue et al. 1995).

Some eastern forest species show idiosyncratic associations with forest type; not all species preferred riparian environments in the Cross Timbers and not all showed the same forest–type preference across other areas of their breeding range. In the Cross Timbers, Black–and–white Warbler, Summer Tanager, Eastern Wood–Pewee, and White–breasted Nuthatch were all found in both riparian and upland forest types. While we found Black–and–white Warblers were weakly associated with upland forests in the Cross Timbers, they were more abundant in riparian

forests in the hardwood forests of Michigan (Bub et al. 2004). Summer Tanager used drier sites more frequently in both the Oklahoma Cross Timbers and Arkansas forests (Wakeley and Roberts 1996). The Eastern Wood–Pewee was weakly associated with riparian forests in the Cross Timbers and more abundant in wetter environments in Arkansas forests, but preferred upland deciduous forests in central Appalachian Mountains (Wakeley and Roberts 1996, Gates and Giffen 1991). The White–breasted Nuthatch was also weakly associated with riparian forests here in the Cross Timbers, it was more abundant in wetter forests in one study in the Arkansas forests, but preferred drier forests in another study from the same region (Smith 1977, Wakely and Roberts 1996).

Two riparian obligate species, Louisiana Waterthrush and Prothonotary Warbler both specialize on nesting and foraging resources available near water. Louisiana Waterthrush nest and forage for aquatic benthic macroinvertebrates along forested streams (Mulvihill, et al 2008). Prothonotary Warbler is a bottomland hardwood species that preferentially selects flooded habitats that have higher food availability compared to dry environments and have more natural nest cavities (Petit and Petit 1996, Hoover 2006). The riparian association we found is characteristic across these species' ranges because of their dependence on stream and water resources. Other eastern species associated with riparian forests in the Cross Timbers are likely responding indirectly to water–resources through the nesting and foraging opportunities related to vegetation structure and composition in riparian microhabitats.

Other studies monitoring nest site selection and nest success suggest that riparian forest characteristics in the Cross Timbers provide better nesting habitat for several eastern forest species. Kentucky warblers are ground nesters that select sites with dense understory vegetation to conceal nests (Kilgo et al. 1996). Green briar, honey–suckle, grape vines, tall grasses, and other low woody and herbaceous vegetation in riparian forests provide more vegetation cover suitable for Kentucky Warbler nests in the Cross Timbers. Acadian Flycatchers are mature

hardwood specialists and nest survival increases with deciduous canopy height (Hazler et al. 2006, Wilson and Cooper 1998). We found that canopy height was significantly taller in riparian forests. Red–eyed Vireos select nest sites with greater canopy coverage (Siepielski et al. 2001) and we found canopy density to be higher in riparian forests.

Assessing food availability is an important mechanism of habitat selection for birds because reproductive success is contingent on food resources. Acadian Flycatchers, for example, select territories with 50% higher arthropod biomass compared to randomly sampled areas within a forest stand (Bakermans and Rodewald 2006). Our results suggest that vegetation structure and composition of riparian forests in the Cross Timbers provide better foraging substrate than upland forests for several selective eastern species. Vegetation structure is correlated with prey density and serves as proximate cue of food availability for insectivorous birds (Seastedt and MacLean 1979, Smith and Shugart 1987). Early in the breeding season while establishing territories, Red–eyed Vireos use foliage density as a proximate cue of future caterpillar availability during the nesting stage because foliage and caterpillar density are positively correlated (Marshall and Cooper 2004). In the Cross Timbers, we found Red–eyed Vireo more frequently in riparian forests, where canopy density is higher, than in adjacent uplands. Kentucky Warbler prefers environments with more ground cover, taller ground cover, and a larger number of woody stems; the dense foliage provides more foraging opportunities for the leaf–gleaning insectivore (Wenny et al. 1993). This species was only detected in riparian forests in the Cross Timbers, where low woody cover and understory density were significantly higher compared to the uplands.

In addition to vegetation structure, tree species composition is an important component of foraging habitat because birds selectively forage on certain species (Holmes and Robinson 1981, Gabbe et al. 2002). Species that are less common or in marginal habitat, like our eastern forest songbirds, are the most selective foragers (Holmes and Robinson 1981). We detected the Yellow–throated Warbler at only two point counts at our eastern–most sites. This species is at

the western extreme of its range in the Cross Timbers and is a highly selective forager that specializes on bald cypress and tupelo in other areas of its range, but likely requires riparian–associated species like bitternut hickory and sycamore in the Cross Timbers (Gabbe et al. 2002). Based on a study in a bottomland forest in Illinois, Yellow–throated Warbler, Summer Tanager, Northern Parula, Prothonotary Warbler, Acadian Flycatcher, and Red–eyed Vireo preferred foraging on American elm, box elder, green ash, and sugarberry (Gabbe et al. 2002). Bitternut hickory was also preferred by several eastern forest species encountered in our study. Bitternut hickory and other tree species selected for by eastern forest songbirds are all associated with riparian forests in the Cross Timbers. Yellow–throated Warbler, Summer Tanager, Northern Parula and Prothonotary Warbler were among the most selective foragers, while Yellow–throated Vireo, Red–eyed Vireo, Tufted Titmouse, Blue–gray Gnatcatcher, Carolina Chickadee, and Yellow–billed Cuckoo were less selective (Gabbe et al 2002). Some of the more selective foragers showed preference for riparian habitat, whereas many of the less selective foragers, the Tufted Titmouse, Blue–gray gnatcatcher, Carolina Chickadee, and Yellow–billed Cuckoo, showed no preference for upland or riparian forests in our Cross Timbers forests.

Differences in vegetation structure and tree species composition suggest that riparian forests in the Cross Timbers provide better foraging habitat for eastern forest species. Our results from invertebrate sampling provide further direct evidence of this. Branch clippings are an accurate method of measuring food availability for foliage–gleaning birds (Johnson 2000). Using this method, we found significantly higher invertebrate abundance in riparian areas compared to uplands. Northern Parula, Kentucky Warbler, Red–eyed Vireo, White–eyed Vireo, and Yellow–throated Vireo are all foliage–gleaning insectivores that may be taking advantage of the higher food availability in riparian foliage. Using Malaise traps, we found a higher average and median aerial arthropod abundance in riparian forests. While the difference was not significant, this may be due to low sample size and high variance of our samples. Other studies using Malaise traps

have found higher food availability in riparian environments compared to adjacent uplands. In the Kansas prairies, insect emergence from streams is greater than terrestrial arthropod production, and the densities of insectivorous birds along streams increase with emergence events (Gray 1989, Gray 1993). In forests of the Pacific Northwest, the abundance of terrestrial invertebrates is greater in riparian areas compared to uplands throughout the breeding season (Hagar et al. 2012).

Our results from the community analysis suggest that upland–riparian forest type is more important at explaining bird community composition than percent forest cover within a 100m- and 1km- radius of surveys. Other studies have found species we encountered in the Cross Timbers sensitive to landscape-level forest cover metrics. In the oak–hickory forests of the Missouri Ozarks, Acadian Flycatcher, Red–eyed Vireo, Yellow–throated Vireo, Carolina Wren, Northern Parula, and Pileated Woodpecker were positively associated with forest cover, whereas Kentucky Warbler, Northern Cardinal, Great Crested Flycatcher, Tufted Titmouse, Eastern Wood–Pewee, Blue–gray Gnatcatcher and Red–bellied Woodpecker were negatively associated with forest cover (Howell et al. 2000). While the species assemblage in the Cross Timbers is similar to the one analyzed in the Ozark forests, broad scale forest cover metrics were secondary to upland–riparian differences in explaining community composition. Upland–riparian dynamics may be more important in the water-limited Cross Timbers forests than broad scale forest patterns important in more mesic oak–hickory forests.

The response of bird communities and species in different environments across their range can be idiosyncratic and region–specific. In the xeric Cross Timbers forests, differences in riparian and upland forest structure and species composition are important in structuring bird communities. Many eastern forest species at the western edge of their breeding range were found more frequently in riparian forests, where the structure and composition of vegetation likely provided better nesting and foraging resources. Our results highlight the mechanisms of riparian–

association for eastern forest songbirds. Riparian forests have higher food availability and better habitat structure; the taller, denser canopies, and the tree species composition and diversity is more similar to eastern deciduous forests compared to adjacent post oak– and blackjack oak–dominated uplands.

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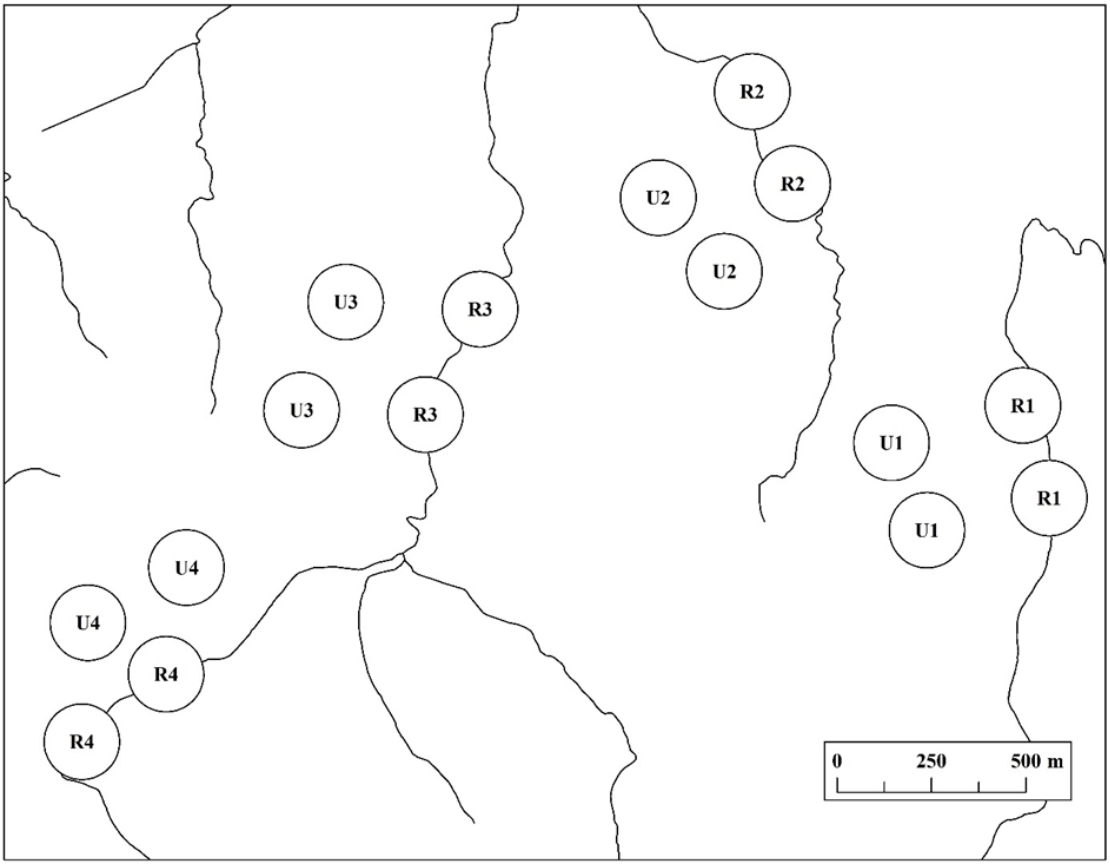

Figure 1. Map of four sites at Okmulgee Wildlife Management Area. Each site (#1-4) consists of two pairs of upland (U) and riparian (R) point counts.

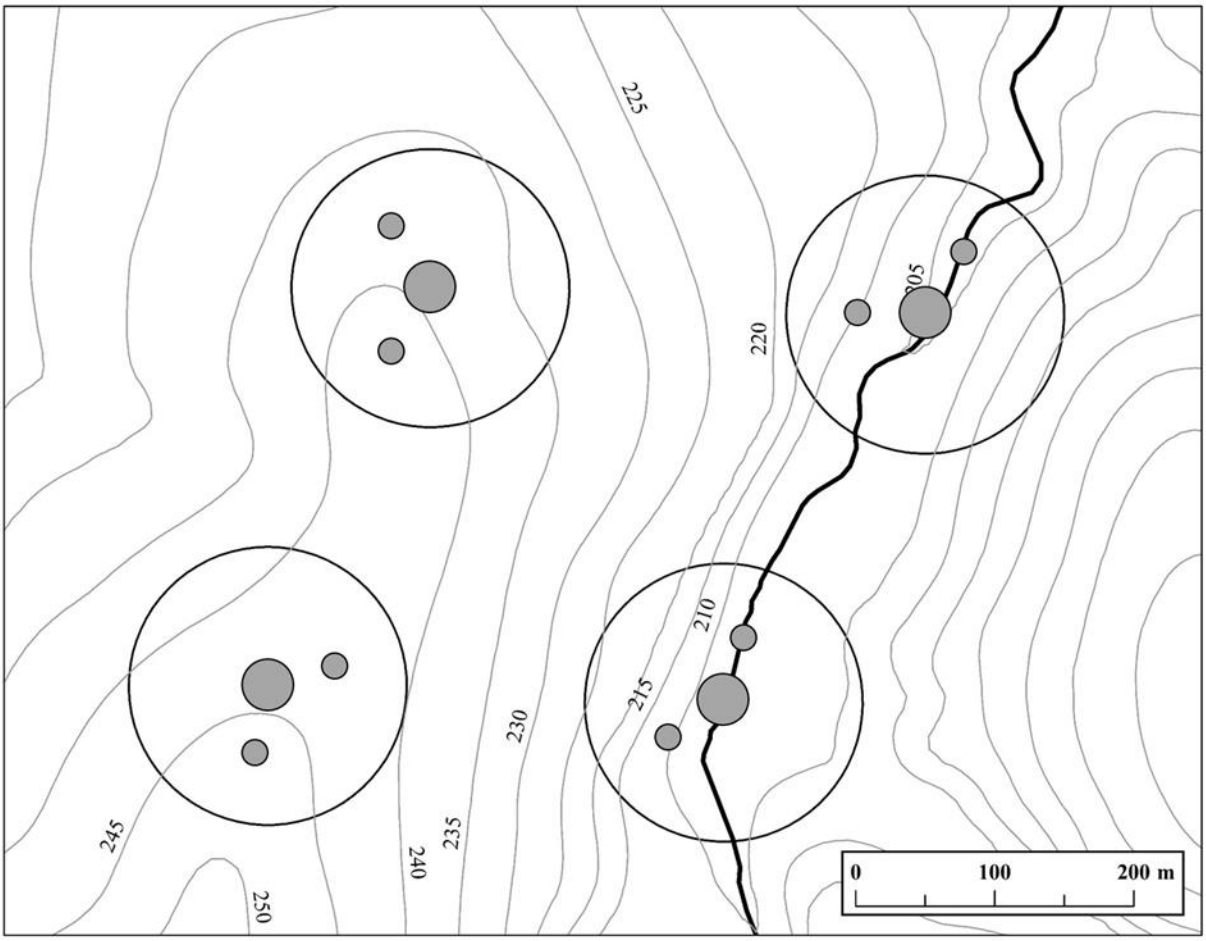

Figure 2. Map of the vegetation plots at Site 3 in Okmulgee Wildlife Management Area. At the center of each point count, there was a 10m-radius vegetation plot where we measured vegetation composition. One 5-m radius vegetation structure plot wass placed at plot center and two were placed 30m from plot center at a 120° angle with one plot along the riparian corridor of riparian sites or uphill from plot center of upland sites

TABLE 1. Tree species associations with riparian and upland forest types.

Common name	Scientific name	Association
Boxelder	*Acer negundo*	Riparian
River birch	*Betula nigra*	Riparian
Bitternut hickory	*Carya cordiformis*	Riparian
Pecan	*Carya illinoinensis*	Riparian
Catalpa	*Catalpa spp.*	Riparian
Sugarberry	*Celtis laevigata*	Riparian
Hawthorn spp.	*Crataegus spp.*	Riparian
Green ash	*Fraxinus pennsylvanica*	Riparian
Kentucky coffeetree	*Gymnocladus dioicus*	Riparian
Black walnut	*Juglans nigra*	Riparian
Osage orange	*Maclura pomifera*	Riparian
Red mulberry	*Morus rubra*	Riparian
American sycamore	*Platanus occidentalis*	Riparian
Eastern cottonwood	*Populus deltoides*	Riparian
Bur oak	*Quercus macrocarpa*	Riparian
Chinkapin oak	*Quercus muehlenbergii*	Riparian
Shumard oak	*Quercus shumardii*	Riparian
Black willow	*Salix nigra*	Riparian
Winged elm	*Ulmus alata*	Riparian
American elm	*Ulmus americana*	Riparian
Slippery elm	*Ulmus rubra*	Riparian
Post oak	*Quercus stellata*	Upland
Blackjack oak	*Quercus marilandica*	Upland
Black oak	*Quercus velutina*	Upland

TABLE 2. Bird species included in the forest community analyses.

Common name	Scientific name	Species code
Barred Owl	*Strix varia*	BADO
Chuck–will's–widow	*Antrostomus carolinensis*	CWWI
Eastern Whip–poor–will	*Anrostomus vociferus*	EWPW
Mourning Dove	*Zenaida macroura*	MODO
Yellow–billed Cuckoo	*Coccyzus americanus*	YBCU
Ruby–throated Hummingbird	*Archilochus colubris*	RTHU
Red–bellied Woodpecker	*Melanerpes carolinus*	RBWO
Downy Woodpecker	*Picoides pubescens*	DOWO
Hairy Woodpecker	*Picoides villosus*	HAWO
Pileated Woodpecker	*Dryocopus pileatus*	PIWO
Eastern Wood–Pewee*	*Contopus virens*	EWPE
Eastern Phoebe	*Sayornis phoebe*	EAPH
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL
Acadian Flycatcher*	*Empidonax virescens*	ACFL
Eastern Kingbird	*Tyrannus tyrannus*	EAKI
White–eyed Vireo*	*Vireo griseus*	WEVI
Bell's Vireo	*Vireo bellii*	BEVI
Red–eyed Vireo*	*Vireo olivaceus*	REVI
Yellow–throated Vireo*	*Vireo flavifrons*	YTVI
Blue Jay	*Cyanocitta cristata*	BLJA
Fish Crow	*Corvus ossifragus*	FICR
American Crow	*Corvus brachyrhynchos*	AMCR
Carolina Chickadee	*Poecile carolinensis*	CACH
Tufted Titmouse	*Baeolophus bicolor*	TUTI
White–breasted Nuthatch*	*Sitta carolinensis*	WBNU
Carolina Wren	*Thryothorus ludovicianus*	CAWR
Blue–gray Gnatcatcher	*Polioptila caerulea*	BGGN
Eastern Bluebird	*Sialia sialis*	EABL
Northern Mockingbird	*Mimus polyglottos*	NOMO
Brown Thrasher	*Toxostoma rufum*	BRTH
Louisiana Waterthrush*	*Parkesia motacilla*	LOWA
Black–and–white Warbler*	*Mniotilta varia*	BAWW
Prothonotary Warbler*	*Protonotaria citrea*	PROW
Kentucky Warbler*	*Geothlypis formosa*	KEWA
Common Yellowthroat*	*Geothlypis trichas*	COYE
Hooded Warbler*	*Setophaga citrina*	HOWA
Northern Parula*	*Setophaga americana*	NOPA

Yellow–throated Warbler*	*Setophaga dominica*	YTWA
Yellow–breasted Chat*	*Icteria virens*	YBCH
Scarlet Tanager*	*Piranga olivacea*	SCTA
Summer Tanager	*Piranga rubra*	SUTA
Field Sparrow	*Spizella pusilla*	FISP
Northern Cardinal	*Cardinalis cardinalis*	NOCA
Indigo Bunting	*Passerina cyanea*	INBU
Painted Bunting	*Passerina ciris*	PABU
Brown–headed Cowbird	*Molothrus ater*	BHCO
Orchard Oriole	*Icterus spurius*	OROR
Baltimore Oriole	*Icterus galbula*	BAOR
American Goldfinch	*Carduelis tristis*	AMGO

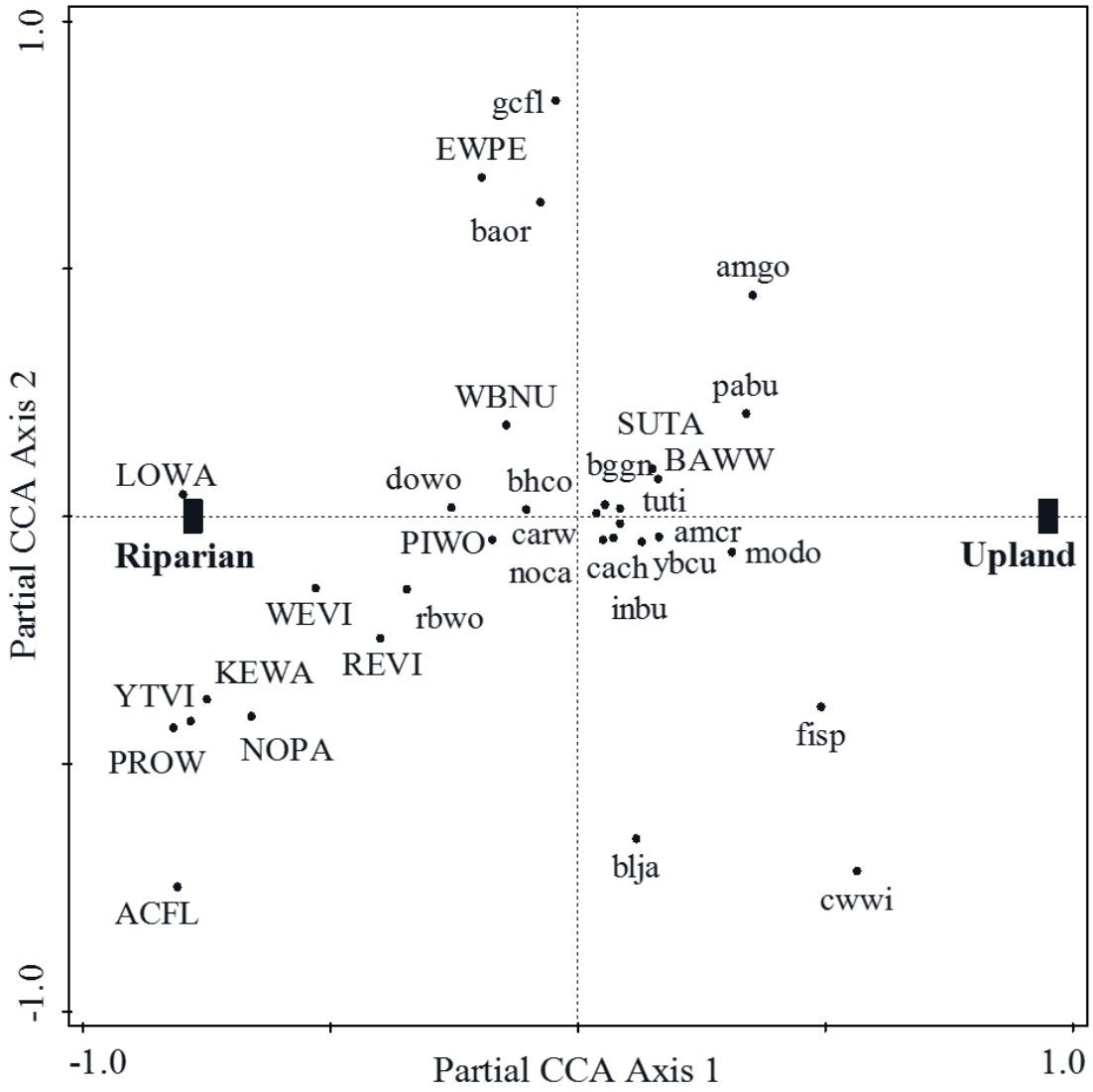

Figure 3. Results of the Canonical Correspondence Analysis (CCA) assessing the influence of upland and riparian forest type on bird communities. Forest type, categorized as upland or riparian, was the only explanatory variable and site was included as a covariate. Eastern forest species of interest are capitalized. Forty-nine species were included in the analysis and the thirty-two most frequently detected species were included in the biplot. Species that used riparian forests more frequently included the riparian obligates, Louisiana Waterthrush (LOWA) and Prothonotary Warbler (PROW), and a few other eastern forest species such as the Acadian Flycatcher, Kentucky Warbler (KEWA), Northern Parula (NOPA), and White–eyed Vireo (WEVI). Field Sparrow (FISP), Painted Bunting (PABU), and American Goldfinch (AMGO) were detected more often in upland forests, and other species such as the Yellow–billed Cuckoo (YBCU), Carolina Chickadee (CACH) and Northern Cardinal (NOCA) showed no preference for upland or riparian forest types.

TABLE 3. Descriptive statistics for vegetation structure and tree species composition comparing bird communities of riparian and upland forests of the Cross Timbers, Oklahoma 2013–2014

Variable	Riparian (n = 91)				Upland (n = 88)				
	Mean	SE	Min	Max	Mean	SE	Min	Max	P
Canopy height (m)*	18.6	0.5	7.8	32.1	11.7	0.5	7.3	15.9	<0.001
Canopy density (%)*	83	2	46	94	69	2	34	93	<0.001
Grass–forb cover (%)*	34	3	3	89	20	3	0	79	<0.001
Understory density (%)*	28	1	5	66	22	1	5	47	<0.001
Low woody cover (%)	23	2	3	85	19	2	4	66	0.086
High woody cover (%)	19	2	2	56	17	2	2	79	0.502
Stand BA (m^2/ha)	24.6	1.4	4.6	77.6	21.9	1.4	8.0	50.4	0.172
Average DBH (cm)	14.3	0.5	7.7	37.8	13.6	0.5	5.8	24.5	0.291
Tree species richness*	6	0.2	1	11	4	0.2	1	10	<0.001
RBA upland oaks (%)*	25.8	3.8	0.0	97.0	74.2	3.8	0.0	100.0	<0.001
RBA riparian trees (%)*	60.0	3.7	0.6	100.0	7.8	3.7	0.0	67.2	<0.001
RBA e. redcedar (%)*	5.1	2.7	0.0	70.7	12.9	2.7	0.0	99.3	0.034

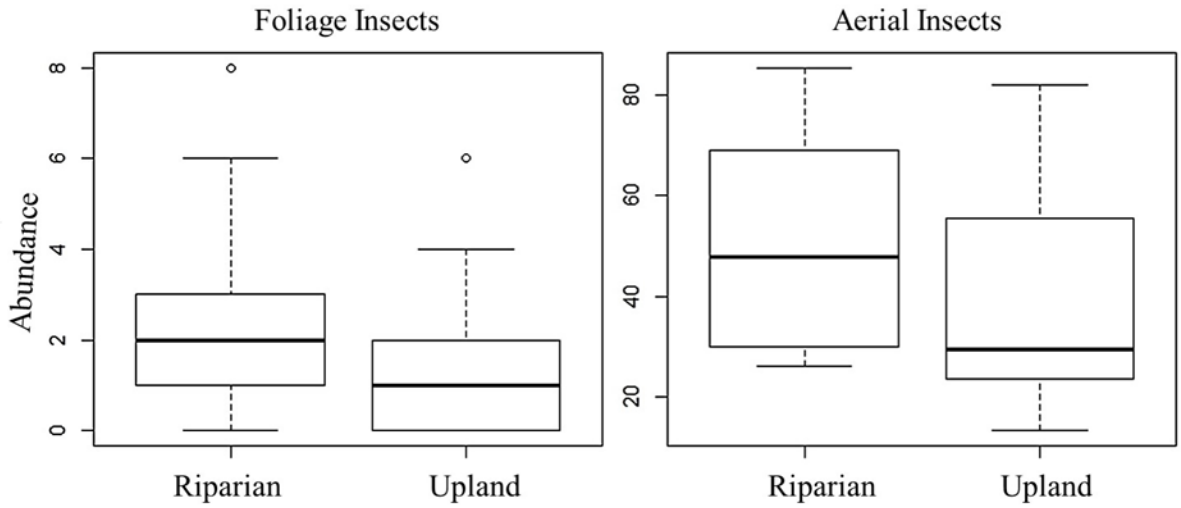

Figure 4. Invertebrate abundance from Malaise traps and branch clippings quantifying food availability in riparian and upland forests.

TABLE 4. Invertebrate summary statistics comparing the abundance and biomass of invertebrates collected from riparian and upland forests.

		Riparian			Upland			
		Mean	± S.E.	N	Mean	± S.E.	N	p–value
Foliage	Abundance*	2.2	0.3	34	1.2	0.2	35	0.017
	Biomass (mg)	12.1	6.6	34	14.9	8.1	35	0.790
Ground	Abundance	1.1	0.2	36	2.2	1.4	37	0.409
	Biomass (mg)	11.6	4.6	36	16.7	10.0	37	0.647
Aerial	Abundance	50.6	8.0	8	39.1	8.5	8	0.341
	Biomass (mg)	360.6	98.2	8	298.0	29.6	8	0.551

TABLE 5. Results of stepwise forward selection with site included as a covariate comparing the relative explanatory power of forest type and forest cover on bird community organization

	Marginal effects % Contribution	Conditional effects % Contribution	P–value (adj)	% Tot. explained
Forest type	76.4	76.4	0.008	8.9
Forest cover – 100 m	28.8	15.6	0.008	1.8
Forest cover – 1 km	19.2	7.9	0.104	0.9
Tot. variation explained				11.6
Adj. explained variation				9.6

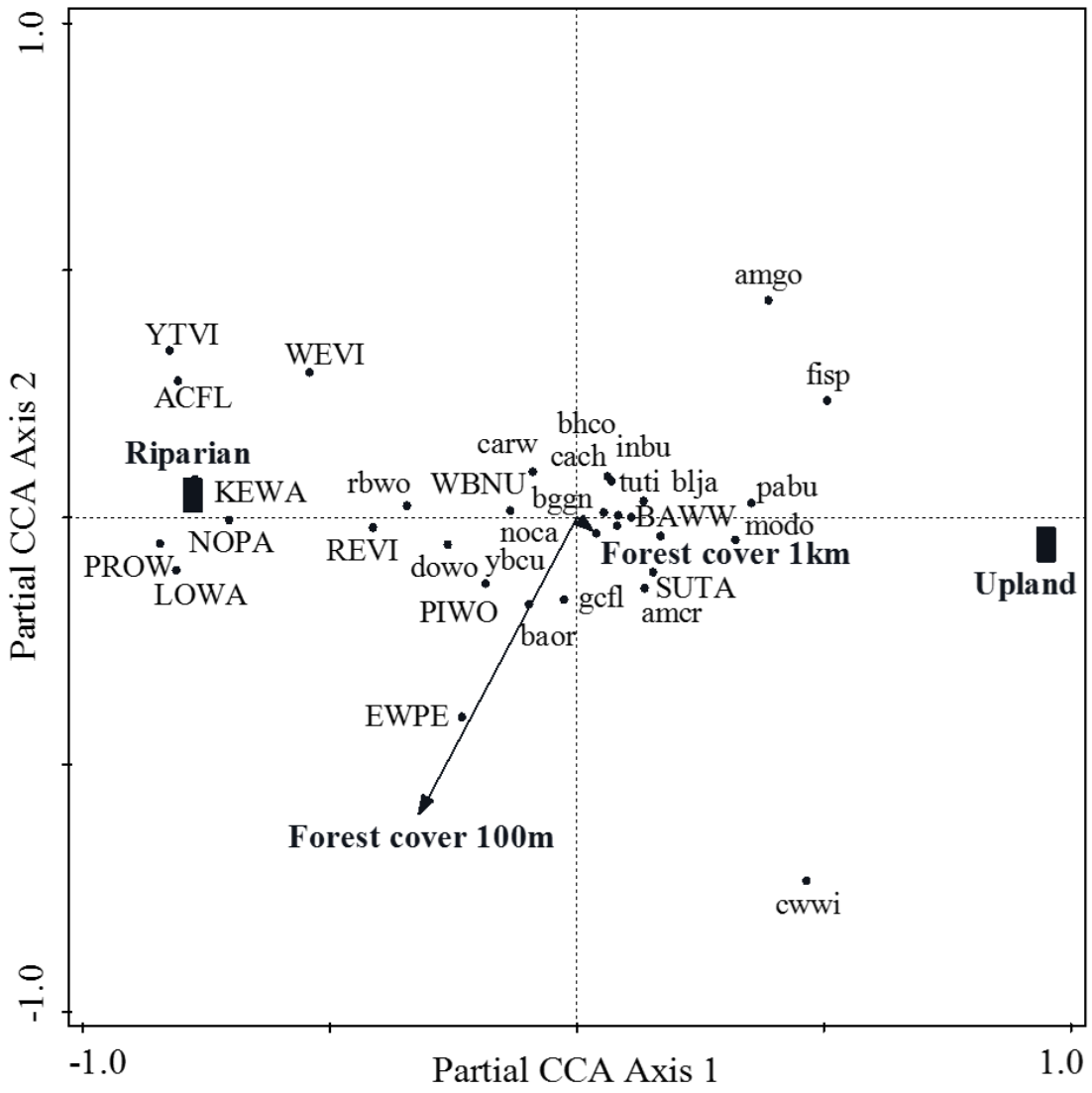

Figure 5. Results of the partial Canonical Correspondence Analysis (pCCA) assessing the influence of forest type and forest cover at the 100m- and 1km- scale on bird communities. Forest type, categorized as upland or as riparian, explained more variation in bird communities than forest cover. 49 species were included in the analysis and the 32 most frequently detected species were included in the biplot.

CHAPTER II

INFLUENCE OF PRECIPITATION AND SURFACE WATER FLOW ON EASTERN FOREST SONGBIRDS AT THEIR WESTERN RANGE LIMIT

INTRODUCTION

Zones of changing temperature and precipitation can mark the boundaries of species distributions and species within communities can respond by expanding into new areas or contracting from these boundaries (e.g., Zuckerberg et al. 2009).). Individuals that occupy sites with prevailing conditions outside their ideal climate niche are likely to be vulnerable to projected changes in temperature and precipitation (Glennon 2014, Thuiller et al. 2005). Our ability to predict how species might respond to projected changes in climate will be important for conservation planning.

The influence of temperature on bird distributions has been well-studied. Analyses from the French Breeding Bird Survey found a 91 km northward shift in bird communities in response to warming temperatures that shifted 273 km northward (Devictor et al. 2008). In Great Britain, the northern range limits of many bird species shifted an average of 18.9 km north (Thomas and Lennon 1999). A similar study in the US using data from the North American Breeding Bird Survey found similar results; the northern range limit of southern bird species analyzed showed a

northward shift of 2.35 km/year (Hitch and Leberg 2006). In New York State, warming temperatures have contributed to an average northern shift of 3.58 km in the mean latitude of 129 species, and an 11.4 km northward shift of the southern range boundaries of primarily boreal species (Zuckerberg et al. 2009).

The influence of precipitation on bird distributions has received comparatively less attention. In the Sierra Nevada Mountains of California, Tingley et al. (2009) found that over a 100 year period, during which the climate became warmer and wetter, 91% of 53 species shifted their distributions based on local climate changes with 40% tracking changes in precipitation, 26% tracking changes in temperature, and 25% tracking changes in both precipitation and temperature. Species tracked either changes in precipitation or temperature based on which climate factor limited NPP (Tingley et al. 2009).

Variation in precipitation affects food resource availability, reproductive success, body condition, and the timing of migration for birds. There is a positive association between seasonal rainfall, food availability, and reproductive success, but nesting success is negatively associated with extreme rainfall events (Morrison and Bolger 2002, Skagen and Adams 2012, Mattson and Cooper 2009). In nonbreeding populations, rainfall is positively associated with food availability, physical condition, and early departure times (Studds and Marra 2007). Thus, there is potential for changes in precipitation to exert a strong influence over distributions, as has been frequently established for temperature.

In the south-central US, there is a marked precipitation gradient that defines the broad ecotone between eastern temperate forest and central grassland biomes. The mesic oak–hickory forests of the Ozark Highlands in eastern Oklahoma transition into a xeric post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*) –dominated Cross Timbers landscape in the central part of the state (Rice and Penfound 1950, Woods et al. 2005). Forests in this region evolved

with periodic drought, fire, and other disturbances that would tend to open the canopy resulting in a mix of oak forest, oak savanna, and tallgrass prairie characterizing the Cross Timbers. Decades of fires suppression and periods of above average precipitation have contributed to the widespread conversion of oak savanna to closed canopy forest patches. A reversal of those climate trends, such as the warmer and drier conditions projected for the Cross Timbers over the coming century (NOAA 2009, Shafer et al. 2014) could again open oak forest canopies through tree mortality in response to drought. Thus, the Cross Timbers is a dynamic transitional ecoregion and well-suited to examining the roles of changing conditions on the distributions of its native organisms.

Multiple species of eastern forest songbirds reach a western distribution limit in the Ozark Highlands and Cross Timbers, with some reaching the western edge of the Cross Timbers and others barely ranging past its eastern boundary (Reinking 2004). Multiple species have expanded into the Cross Timbers over the past several decades. Some of these species might be expanding into a broad area of usable habitat that presents opportunities for population growth. Others species might be attracted to ecological traps (e.g. Leston and Rodewald 2006) in apparently suitable patches where, at the edge of their range, hospitable conditions in one season could be inhospitable in the next.

To better understand community-level responses of breeding birds and identify species sensitive to fluctuating precipitation, we examined how these communities and species responded to the current spatial precipitation gradient. Our objectives were to examine how bird communities respond to forest cover and surface water patterns along a precipitation gradient, and examine how potentially sensitive species at the edge of their breeding ranges are affected by forest cover and surface water patterns in the Ozark Highlands and Cross Timbers. We hypothesize that eastern forest species will be more positively associated with areas of higher flow accumulation in the more arid Cross Timbers ecoregion.

METHODS

Study Area.— The study area spanned two ecoregions of eastern and central Oklahoma: the Ozark Highlands and Cross Timbers. There is a dramatic precipitation gradient across the study's extent and forest structure and composition are shaped by this east–west cline. The oak–hickory forests of the Ozark Highlands transition to the more xeric Cross Timbers characterized by open low-growing stands dominated by post (*Quercus stellata*) and blackjack (*Q. marilandica*) oaks (Rice and Penfound 1959). Forests in the Ozark Highlands occur on hills and mountains, whereas low–lying and flat terrain has been largely converted to agricultural land uses (Woods et al. 2005). Oak–hickory forests characteristic of the eastern US dominate the Ozark Highlands; dominant species include black hickory (*Carya texana*), mockernut hickory (*Carya tomentosa*), winged elm (*Ulmus alata*), sugar maple (*Acer* saccharum), post oak (*Quercus stellata*) white oak (*Q. alba*) (Rice and Penfound 1959). As precipitation decreases westward, upland forests become more open, tree species diversity decreases, and average tree height and basal area decrease. Although oak savanna structure characterized much of the Cross Timbers historically, fire suppression in recent decades has resulted in higher stem densities and a shift in species composition such that eastern redcedar (*Juniperus virginiana*), elms (*Ulmus spp.*), black hickory (*Carya texana*), and red mulberry (*Morus rubra*) have increased since the 1950s (DeSantis et al. 2010). Riparian zones within Cross Timbers forests also support overstory species such as cottonwood (*Populus deltoides*), sugarberry (*Celtis laevigata*), and green ash (*Fraxinus pennsylvanica*) (Hoagland 1998).

Bird Surveys.— We used breeding bird community data from two independent field studies to analyze responses to water availability along a precipitation gradient. Both studies used point-count methods for bird community surveys and presence-absence was used as the unit of analysis for this study. The first study was conducted in 2006 and 2007 in the Ozark Highlands of eastern Oklahoma (Cavalieri et al. 2009). We used bird community data from 135

point counts at 34 sites. Each site was arranged as a 1km transect with four point counts spaced at 250m. Bird communities were surveyed once within 100m fixed–radius point counts for 6–minutes (Ralph et al. 1993). Using these two independent datasets for our analysis was reasonable because there was little change in the landscape over the 7 year gap between the two studies. There is annual variation in community composition at specific point count locations, but it is unlikely that overall community composition changes in the short term.

The second study occurred in 2013 and 2014 in the Cross Timbers of central Oklahoma. A total of 179 point counts from 45 sites were included in this analysis. Sites were arranged as paired upland–riparian point counts; each site included two point counts along streams and two nearby upland point counts separated by at least 50m. Like the study in eastern Oklahoma, bird communities were surveyed within a 100m–fixed radius point count, however each point count was surveyed twice for 8–minutes within a single field season (Ralph et al. 1993).

Environment. – Climate, surface water flow, and land cover information were all gathered using GIS in ArcMap 10.2.1 (ESRI, Redlands, California, USA). Annual precipitation was obtained from PRISM Climate Group models (Parameter–elevation Regressions on Independent Slopes Model). These models used point data, digital elevation models, and climate averages from 1981–2010 to interpolate annual precipitation continuously across the landscape. From these continuous raster datasets, we identified annual temperature and precipitation at each survey location (PRISM Climate Group 2014). Percent forest cover within 1km of each study site was calculated using the 2006 National Land Cover Dataset (Fry et al. 2011). Forest cover included all types—deciduous, coniferous, mixed forests, and wooded wetlands.

Surface water availability was estimated for every point count by calculating flow accumulation. Flow accumulation is the amount of upland area draining through a location and quantifies a continuous upland-riparian gradient. Flow accumulation is derived from a region's

topography and was calculated using 30m Digital Elevation Models (Gesch et al. 2002). Based on the relative elevation of each pixel in a DEM, a direction of surface water flow was assigned to every pixel. From the flow direction output raster we limited the area from which we calculated flow accumulation to the HUC–12 watershed level. These are the smallest standard class of watersheds and range from approximately 7,000 to 12,000 ha in the Cross Timbers. Maximum flow accumulation for each point count was used as our predictor variable; this value was log transformed because of its skewed distribution (Figure 1.).

Data Analysis.– Our objectives were to examine the influence of precipitation, forest cover, and flow accumulation on forest bird communities and eleven focal species. First we compared our predictor variables between the Ozark Highlands and Cross Timbers using One–Way ANOVA. We then used canonical correspondence analysis (CCA) to conduct a bird community analysis across the entire extent of our study. Finally we used presence–absence data for eleven eastern forest songbirds to evaluate their responses to precipitation, flow, and forest cover using generalized linear models.

Analysis of bird communities and focal species. –We used ordination techniques to evaluate the forest bird community's response to precipitation, forest cover, and flow accumulation across Oklahoma's transitional forested landscape. Explanatory variables analyzed included long term annual precipitation, percent forest cover within 1km of each study site, and maximum flow accumulation values at each point count. We used CCA to assess the influence and relative importance of these environmental variables on multiple response variables simultaneously (Ter Braak 1986, Palmer 1993). We evaluated the explanatory power of each environmental variable on songbird community variation using forward selection. All analyses were conducted in the program CANOCO 5.03.

We employed an information–theoretic approach to examine how surface water flow, forest cover, and annual precipitation explain the occurrence of eastern forest songbirds from the Ozark Highlands through the Cross Timbers. Presence–absence data for eleven species from the two independent bird community surveys were analyzed as binary response variables using generalized linear models. These species include Acadian Flycatcher, Eastern Wood–Pewee, Red–eyed Vireo, White–eyed Vireo, Yellow–throated Vireo, Northern Parula, Kentucky Warbler, Black–and–white Warbler, Prothonotary Warbler, Louisiana Waterthrush, and Summer Tanager (Appendix Table 6.). Parameters used in the models included annual precipitation based on long term climate data, percent forest cover within 1km of surveyed sites, and flow accumulation (Table 1.). For every species, a full set of models was run for the Cross Timbers ecoregion, the Ozark Highlands, and the full extent of the study. This allowed comparisons of the relative importance of precipitation, forest cover, and flow in areas of lower rainfall, higher rainfall, and across the full precipitation gradient. Models tested for these eastern forest species included a null model, where the intercept was the only parameter, a full model with all predictor variables, and all possible combinations of forest, flow, and precipitation variables. Every candidate model for each species included exactly the same data. Model performance was assessed based on AIC rankings.

RESULTS

Comparison of ecoregions. – Average annual precipitation between 1980 and 2010 was higher in the Ozark Highlands (mean = 121.1 cm/yr ± 0.7 SE) than in the Cross Timbers (mean = 99.1 cm/yr ± 0.4 SE) ($p < 0.01$, One–Way ANOVA; Table 2.). Forest cover within 1km of each site was greater in the east (mean = 81.8% ± 1.1 SE) than the west (mean = 66.0% ± 1.1 SE) ($p = <0.01$, One–Way ANOVA; Table 2.) and ranged from 43.5% to 96.4% in the Ozark Highlands and 32.6% to 93.1% in the Cross Timbers. Forest cover was correlated with annual precipitation and so we expected significantly less forest cover in the western ecoregion, where annual

precipitation is lower. Flow accumulation, however, was not correlated with either precipitation or forest cover variables (Figure 2.). The range of values for flow accumulation of point counts were similar between eastern (0.301–4.887) and western (0.301–4.812) point counts, but the difference in average flow values was nearly significant ($p = 0.052$, One–Way ANOVA; Table 2.).

Bird community responses. – We included 69 species in the bird community analysis using CCA; the 35 most frequently encountered species were included on the biplot (Figure 2.). For the entire study extent, the adjusted variation explained by annual precipitation (in/yr), percent forest cover within 1km of a site, and flow accumulation was 7.7%. The marginal and conditional effects of the three explanatory variables on bird communities are summarized in Table 3. Forward–selection results on this CCA found that annual precipitation contributed 58.3% of total explained variation ($p = 0.006$), flow accumulation contributed 28.7% ($p=0.006$), and percent forest cover contributed 13.0% ($p=0.006$) after accounting for covariation between the three explanatory variables. We adjusted p–values from the forward selection results using Holm's correction. Forest cover and precipitation were correlated across the study extent, but flow accumulation was orthogonal to these two covariates (Figure 2.; Table 3.).

Eastern forest songbirds showed mixed responses to the three environmental gradients tested. Pine Warbler (PIWA), Scarlet Tanager (SCTA), and Yellow–Breasted Chat (YBCH), were three species limited to areas of higher precipitation (Figure 2.). Louisiana Waterthrush (LOWA) and Prothonotary Warbler (PROW) were found in areas of higher flow accumulation, but did not respond to the precipitation gradient; these riparian obligate species were found across the study extent (Figure 2.). Yellow–throated Vireo (YTVI), Northern Parula (NOPA), and Kentucky Warbler (KEWA) responded positively to precipitation, forest cover, and flow accumulation in the CCA (Figure 2.). The species scores for Black–and–white Warbler and Summer Tanager were near–center on the biplot indicating no strong responses to the three

environmental gradients tested. Other species that were either widely distributed, generalists, or not strongly associated with forest cover showed little response to the environmental gradients. These species included Tufted Titmouse (TUTI), Great Crested Flycatcher (GCFL), Carolina Wren (CARW), and Northern Cardinal (NOCA) among others.

Focal species responses. – Results of the top models explaining the occurrence of eastern forest species in the Ozark Highlands and Cross Timbers based on precipitation, forest cover, and flow accumulation are summarized in Table 4. All of the top models ($\Delta AIC \leq 2$) are listed in the appendix.

Based on results from the GLM models, the focal eastern forest songbirds responded differently to precipitation, forest cover, and flow accumulation at the full extent of the study (Table 4). The top models for Yellow–throated Vireo, Northern Parula, Kentucky Warbler, Red–eyed Vireo, and White–eyed Vireo were positively associated with forest cover and flow accumulation. The top model for Acadian Flycatcher showed a positive response to both precipitation and flow. The top models for Louisiana Waterthrush and Prothonotary Warbler, our two riparian–obligate species, showed a positive response to flow accumulation and a negative response to precipitation. Unlike other eastern forest species, Eastern Wood–Pewee, Black–and–white Warbler, and Summer Tanager did not show positive associations with either precipitation or flow accumulation. The top models for Black–and–white Warbler and Summer Tanager were negatively associated with both precipitation and flow (although Summer Tanager was positively associated with percent forest cover). The null model was top-ranked for Eastern Wood–Pewee across the full study extent. The second–best ranked model for this species showed a positive association with precipitation; the precipitation model had a ΔAIC of 0.20 and an AIC weight of 0.2431.

Top–ranked models from the Ozark Highlands and Cross Timbers ecoregions for each species indicated that the best predictors of species occurrence differed between the two ecoregions (Table 4.). Models from the west using flow accumulation alone had higher rankings and higher Akaike weights than those in the east for Acadian Flycatcher, Red–eyed Vireo, Northern Parula, Kentucky Warbler, White–eyed Vireo, Eastern Wood–Pewee, Prothonotary Warbler and Louisiana Waterthrush (Table 5.). In other words, flow accumulation was a better predictor of these species' presences in the Cross Timbers than it was in the Ozark Highlands. For Red–eyed Vireo, forest alone was the best predictor of species presence in the wetter climate of the eastern Ozark Highlands, while the best model included forest and flow accumulation in the more arid western Cross Timbers (Table 4.). In the east, the top model for the Northern Parula was the full model and the top models for Kentucky Warbler and White–eyed Vireo showed positive associations with forest and flow. In the Cross Timbers, the top models for these three species showed positive associations for flow accumulation alone (Table 4.). Both Acadian Flycatcher and Yellow–throated Vireo had a positive association with precipitation and flow accumulation in the Cross Timbers (Table 4.). These species were not found in the driest most western sites of the Cross Timbers surveys; we surveyed beyond the western extent of their breeding range. Because of this, they showed positive associations with precipitation within the Cross Timbers ecoregion. Our riparian obligates, Louisiana Waterthrush and Prothonotary Warbler were both positively associated with flow in the eastern and western ecoregions (Table 4.). Eastern Wood–Pewee, Summer Tanager, and Black–and–white Warbler showed mixed results across and between ecoregions (Table 4.). Based on the results of the CCA (Figure 2.) these species were not expected to respond strongly to the precipitation, forest cover, and flow environmental variables.

DISCUSSION

Many studies of eastern forest songbirds have emphasized the importance of forest landscape patterns, forest structure, and floristics on species diversity, community composition, and on the abundance of sensitive species (Flather and Sauer 1996, Howell et al. 2000, Mitchell et al. 2001, Mitchell et al. 2006, Lynch and Whigham 1984, Boulinier et al. 2001, Lee and Rotenberry 2005). Our analysis of forest bird communities incorporates water resources in addition to forest cover. The most striking results of our analyses are the importance of precipitation and surface water patterns on forest songbird communities and eastern forest species in particular.

We investigated the response of forest birds to two moisture gradients across a transitional forested landscape. We looked at the importance of surface water patterns across a precipitation gradient on community composition and species occurrences. Flow accumulation and precipitation are important to birds because of the associated changes in vegetation along the soil moisture gradient. Flow accumulation is a measure of how much surface water drains across a specific location based on landscape topography. It is a continuous variable representing an upland-riparian gradient. Uplands have low flow accumulation, whereas stream channels have higher flow accumulation because surface water from uplands concentrates in these lowland drainages. Across an approximately 250 km east–west study extent, precipitation was the most important environmental variable organizing bird communities. The second most important variable was flow accumulation. While forest cover was significant in explaining variation in the forest bird community, it was not as important as precipitation and flow accumulation.

Based on a community–level analysis, we found some forest bird species were limited to regions of higher precipitation and others were limited to regions of higher flow accumulation. Scarlet Tanager, Yellow–breasted Chat, Pine Warbler, and Yellow–throated Warbler were limited to areas of higher precipitation near the eastern edge of our study area. The second moisture gradient, flow accumulation, was used to examine the effects of surface water patterns on forest

bird communities. The distributions of Louisiana Waterthrush and Prothonotary Warbler were not limited by the east–west precipitation gradient, but they did respond positively to flow accumulation. Yellow–throated Vireo, Northern Parula, and Kentucky Warbler were positively associated with both moisture gradients across the study extent.

The species sensitive to the precipitation or surface water gradients shared life history traits such as long-distance migration, obligate insectivory, and single-broodedness. These traits tend to make such species more sensitive to landscape structure of forests than, for example, residents and short–distance migrants (Flather and Sauer 1996, O'Connell et al. 2000). In contrast, other species widely distributed across the eastern deciduous forests and prairies of the region did not respond strongly to either moisture gradient. These forest generalists, including Tufted Titmouse Yellow–billed Cuckoo and Blue–gray Gnatcatcher, were less sensitive to changes in land cover (Howell et al. 2000).

In order to identify changes in habitat associations in regions of higher and lower rainfall, we compared models of species occurrences in the Ozark Highlands with those in the Cross Timbers. High flow accumulation was a better predictor of occurrences for Acadian Flycatcher, Red–eyed Vireo, Northern Parula, Kentucky Warbler, White–eyed Vireo, and Eastern Wood–Pewee in the Cross Timbers than in the Ozark Highlands. In other words, these facultative riparian forest species rely more on riparian forests where water from precipitation is more limiting. Our findings are similar to those found in Australia's tropical savanna along a similar broad–scale precipitation gradient; riparian vegetation is more suitable for species typically found in areas of higher rainfall and allows these species to inhabit drier savanna–type environments (Woinarski et al. 2000).

Examining the influence of precipitation and flow accumulation in shaping bird species distributions is important when considering historical bird population trends and the implications

of projected increases in temperature and declines in precipitation for the southern Great Plains. Droughts in the 1930s and 1950s caused tree mortality in western and central Oklahoma's uplands forests (Rice and Penfound 1959). These severe droughts would have made regional conditions unsuitable for eastern forest songbirds. Between 1980 and 2010, Oklahoma has seen an unusually wet climate (Basara et al. 2013). Fire suppression has also changed forest composition and structure since the 1950s; stand density has increased and mesophytic species such as elms (*Ulmus spp.*), red mulberry (*Morus rubra*), and eastern redcedar (*Juniperus virginiana*) have expanded further west into the Cross Timbers (DeSantis et al. 2010). Based on Breeding Bird Survey population trend maps, since 1966 populations of several eastern forest species have increased with trends in higher precipitation, fire suppression, the expansion of mesophytic tree species, and increases in forest stand density. These species include Eastern Wood-Pewee, Eastern Phoebe, Great Crested Flycatcher, White-eyed Vireo, Yellow-throated Vireo, Red-eyed Vireo, White-breasted Nuthatch, Carolina Wren, Black-and-white Warbler, Northern Parula, Pine Warbler, Yellow-breasted Chat, Summer Tanager, Northern Cardinal, and Indigo Bunting (Sauer et al. 2012). Projected temperature increases, precipitation declines, and more frequent and severe droughts in the region may cause a reversal of these species' expansions.

Oklahoma has experienced periodic extended severe droughts in the 1930s and 1950s. The summer of 1936 was the warmest summer on record for the Great Plains and 1956 was the driest year (Krunkel et al. 2013). In the 1950s, drought stress caused significant tree mortality especially in the western prairies and central oak–savannas of Oklahoma (Rice and Penfound 1959). Drought events have also been responsible for oak mortality in the savannas of Minnesota and oak decline in the Ozarks of Missouri (Faber–Langendoen and Tester 1993, Voelker et al. 2008). Other studies in woodlands and savannas provide evidence for the potential of broad-scale tree mortality due to drought. Warmer temperatures cause drought stress which accelerates

drought–induced mortality, increases average background mortality rates, and can cause rapid and extensive change in forest cover across a landscape (Adams et al. 2009, Van Mantgem and Stephenson 2007, Van Mantgem et al. 2009).

Several characteristics make the Cross Timbers vulnerable to widespread forest die–off and ecotype shifts. Water–limited forests near species range margins are more vulnerable to mortality (Allen et al. 2010). Temperature increases and severe droughts, like the ones projected for the southern Great Plains, can cause regional die–off of overstory trees and rapid and extensive shifts in woodland ecotones (Breshears et al. 2005, Allen and Breshears 1998). Higher soil moisture losses under open–canopy oak savannas due to increased evapotranspiration may make these forest types more vulnerable than woodlands and closed–canopy forests to drought mortality (Faber–Langendoen and Tester 1993). Conversely, higher stand density increases competition for water and exacerbates drought stress and mortality (Allen and Breshears 1998). Fire suppression and a relatively moist climate over the past 30 years have caused an increase in basal area and tree density in the Cross Timbers forests (Desantis et al. 2010).

After surveying upland oak forests following severe drought in the 1950s, Rice and Penfound (1959) predicted that under a drier climate, oak savannas would transition into grasslands and oak–hickory forests would transition into oak savannas. Species that currently show sensitivity to precipitation and surface water patterns will likely track future ecotone shifts that are projected to occur based on climate change models. Based on current species distributions across the Ozark Highlands and Cross Timbers ecoregions, eastern forest species such as the Yellow-throated Vireo, Acadian Flycatcher, Yellow-breasted Chat and Kentucky Warbler will be vulnerable to changes in forest structure and composition associated with precipitation patterns. In water-limited environments, surface water patterns may be more important in organizing species distributions than in areas of higher precipitation.

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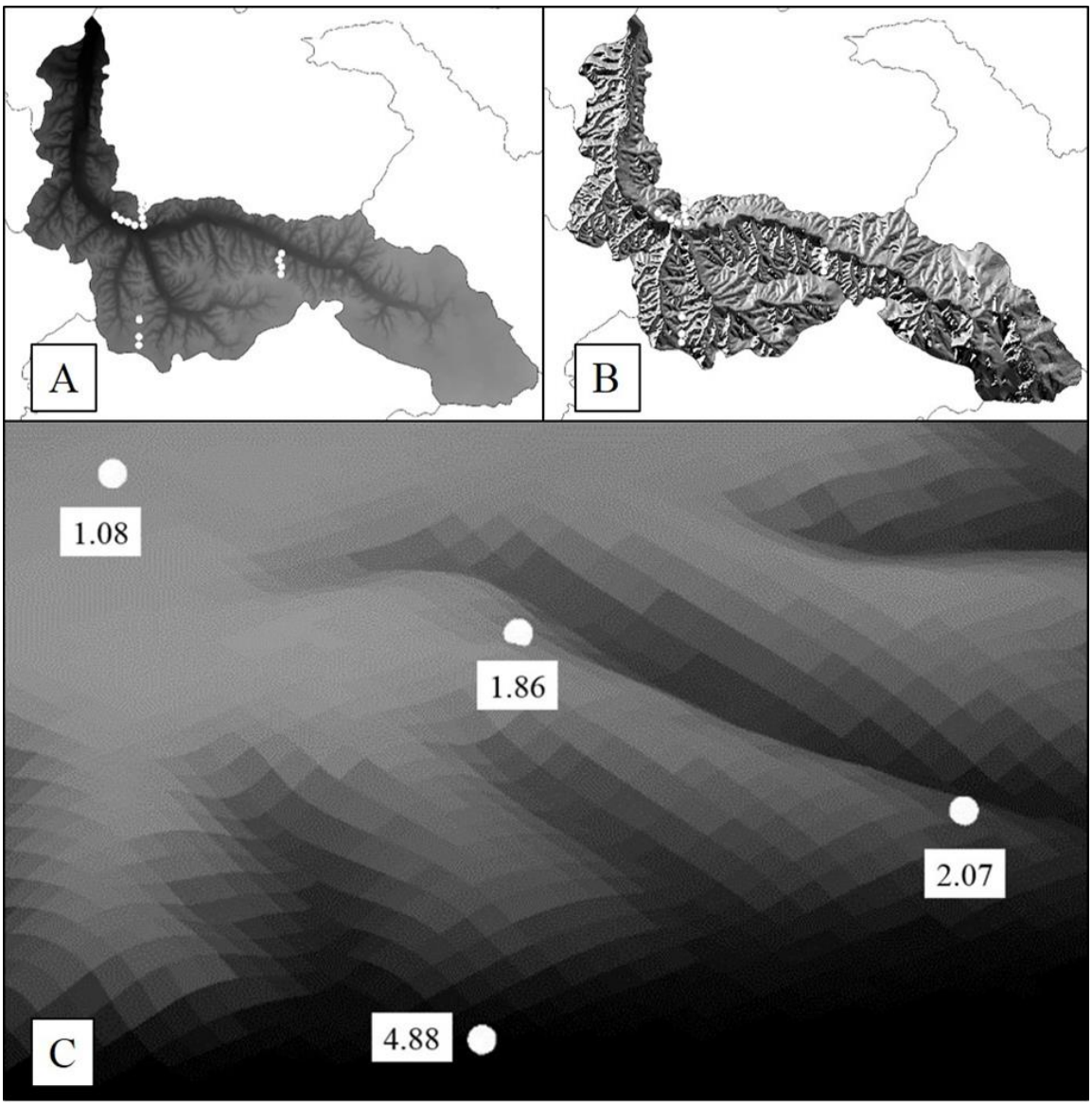

Figure 1. Flow accumulation calculated for each point count. Flow accumulation is based on a locations topography and elevation relative to surrounding cells. From 30m DEM at the HUC-12 watershed (A) the direction of surface water flow was predicted (B) and then a flow accumulation value was calculated for each pixel based on how many upland pixels drain into that area (C).

Table 1. Summary of the parameters used in the models to predict presence–absence in eastern forest songbirds

Parameter	Description
PA	Presence–absence species' binary response variable
β_0	Fixed intercept
PRCP	Annual precipitation (in/yr), 1981–2010 PRISM data
FRST	Percent forest cover within 1km of each site, 2006 NLCD
FLW	Log(maximum flow accumulation) of each point count, 30m DEM

Table 2. Descriptive statistics by ecoregion for predictor variables by included in the generalized linear models examining the presence–absence of eastern forest songbirds along a precipitation gradient

	Ozark Highlands (n=135)		Cross Timbers (n=179)		
Predictor variable	Mean	SE	Mean	SE	p–value
Flow accumulation	1.84	0.09	2.09	0.09	0.053
Annual precipitation (cm/yr)	121.1	0.7	99.1	0.4	<0.001
Forest cover (%)	81.8	1.1	66.0	1.1	<0.001

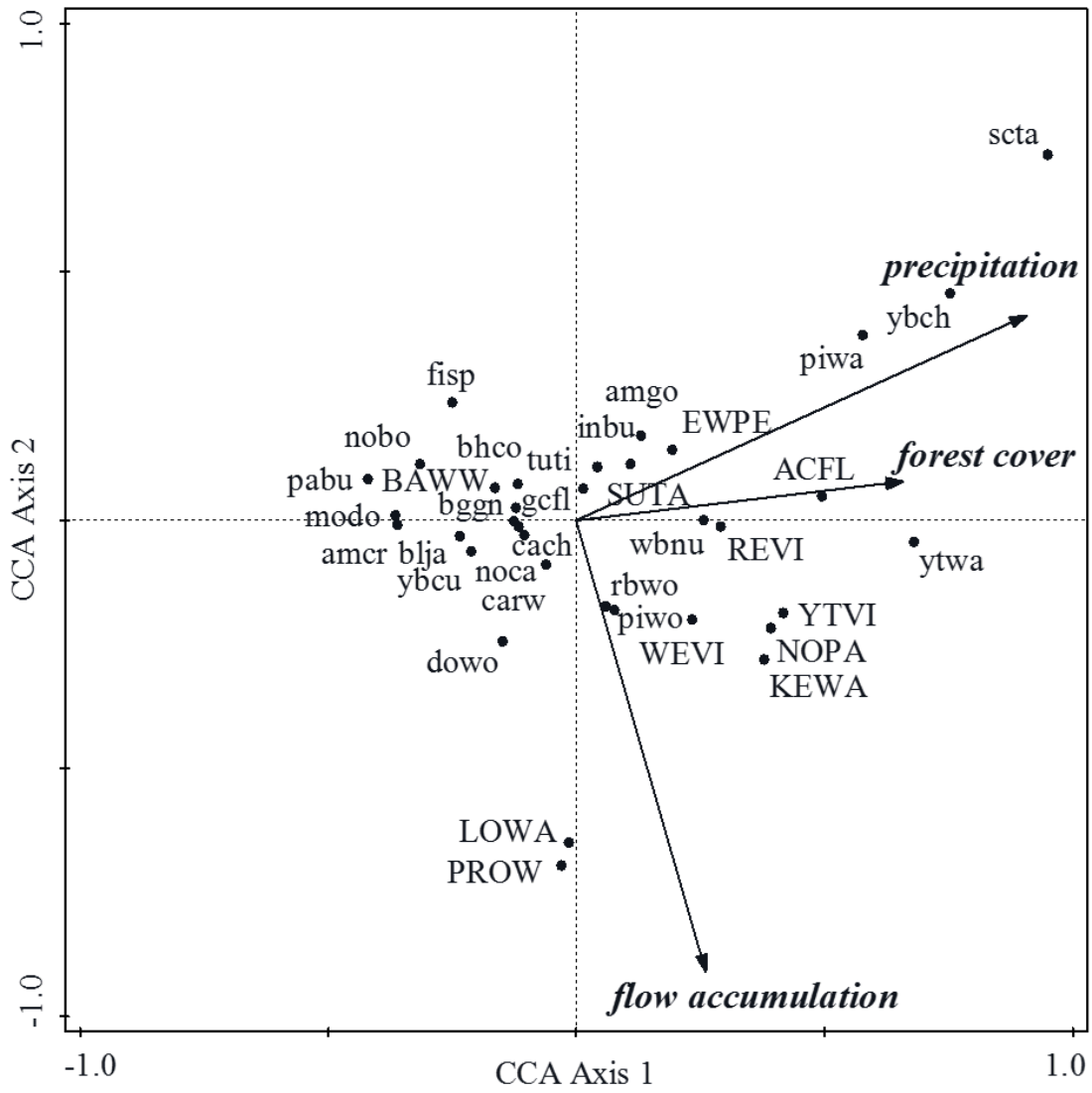

Figure 2. Canonical Correspondence Analysis (CCA) biplot results assessing the influence of precipitation, forest cover, and flow accumulation on bird communities of the transitional landscape of the Ozark Highlands, and Cross Timbers ecoregions of Oklahoma. The 35 most frequently encountered species are displayed. Species capitalized are the focal species analyzed using generalized linear modeling.

TABLE 3. Marginal and conditional effects of annual precipitation, forest cover, and flow accumulation on the percent variation of bird communities explained

	Marginal effects	Conditional effects		
	% Contribution	% Contribution	P-value (adj)	% Tot. explained
Annual precipitation	58.3	58.3	0.006	5.0
Forest cover - 1km	34.0	13.0	0.006	1.1
Flow accumulation	26.0	28.7	0.006	2.5
Tot. variation explained				8.6
Adj. explained variation				7.7

Table 4. Summary of the top AIC–selected models predicting species occurrence in the Ozark Highlands (east), the Cross Timbers (west), and the entire study extent (e + w). Parameters are described in table 1. N = number of sites at which a species was present

Species	N	Extent	PRCP	FRST	FLW	df	LogLik	AIC	ΔAIC	AIC wt
ACFL	54	e + w	+		+	3	–130.32	266.64	0.00	0.7098
	41	east	–			2	–79.94	163.88	0.00	0.4139
	13	west	+		+	3	–34.64	75.28	0.00	0.6474
YTVI	17	e + w		+	+	3	–61.23	128.46	0.00	0.4568
	7	east				1	–27.53	57.06	0.00	0.2210
	10	west	+		+	3	–31.54	69.08	0.00	0.5415
NOPA	96	e + w		+	+	3	–153.22	312.44	0.00	0.5120
	57	east	–	+	+	4	–70.39	148.78	0.00	0.9636
	39	west			+	2	–70.64	145.29	0.00	0.2935
KEWA	59	e + w		+	+	3	–127.71	261.42	0.00	0.6571
	31	east	+	+		3	–65.15	136.30	0.00	0.4174
	28	west			+	2	–60.60	125.19	0.00	0.3864
REVI	157	e + w		+	+	3	–192.73	391.45	0.00	0.7065
	79	east		+		2	–82.06	168.12	0.00	0.5013
	78	west		+	+	3	–100.57	207.14	0.00	0.5996
WEVI	67	e + w		+	+	3	–149.31	304.62	0.00	0.4453
	28	east		+	+	3	–64.14	134.28	0.00	0.4066
	39	west			+	2	–85.12	174.24	0.00	0.4463
EWPE	79	e + w	–			1	–177.12	356.24	0.00	0.2683
	43	east	–		–	3	–80.85	167.70	0.00	0.3819
	36	west			+	2	–88.77	181.54	0.00	0.2589
BAWW	91	e + w	–		–	3	–175.52	357.03	0.00	0.4513
	20	east	+			2	–54.25	112.50	0.00	0.3805

	71	west	–	+		3	–111.65	229.29	0.00	0.3094
LOWA	32	e + w	–		+	3	–72.43	150.86	0.00	0.6859
	3	east			+	2	–10.37	24.75	0.00	0.4594
	29	west			+	2	–60.84	125.67	0.00	0.4647
PROW	16	e + w	–		+	3	–47.40	100.79	0.00	0.6253
	1	east			+	2	–4.55	13.09	0.00	0.2936
	15	west			+	2	–42.11	88.22	0.00	0.5077
SUTA	171	e + w	–	+	–	4	–208.90	425.80	0.00	0.5540
	66	east	–	+		3		169.82	0.00	0.6212
	105	west	+		–	3	–116.90	239.80	0.00	0.3968

Table 5. Summary comparing flow–only models predicting species presence–absence in the Ozark Highlands (east) and the Cross Timbers (west). N = number of sites at which a species was present; R = model rank.

Species	N	Extent	R	FLW	LogLik	AIC	ΔAIC	AIC wt
ACFL	41	east	6	+	–82.11	168.21	4.335	0.0474
	13	west	3	+	–38.17	80.33	5.052	0.0518
YTVI	7	east	2	+	–26.72	57.44	0.375	0.1833
	10	west	6	+	–36.68	77.37	8.284	0.0086
NOPA	57	east	4	+	–78.59	161.18	12.401	0.0020
	39	west	1	+	–70.64	145.29	0.000	0.2935
KEWA	31	east	3	+	–67.47	138.93	2.637	0.1117
	28	west	1	+	–60.60	125.19	0.000	0.3864
REVI	79	east	7	+	–91.56	187.13	19.014	0.0000
	78	west	3	+	–103.68	211.37	4.233	0.0722
WEVI	28	east	2	+	–65.52	135.04	0.760	0.2780
	39	west	1	+	–85.12	174.24	0.000	0.4463
EWPE	43	east	6	–	–83.68	171.36	3.654	0.0614
	36	west	1	+	–88.77	181.54	0.000	0.2589
BAWW	20	east	6	–	–56.06	116.12	3.620	0.0623
	71	west	6	–	–119.56	243.12	13.834	0.0003
LOWA	3	east	1	+	–10.37	24.75	0.000	0.4594
	29	west	1	+	–60.84	125.67	0.000	0.4647
PROW	1	east	1	+	–4.55	13.09	0.000	0.2936
	15	west	1	+	–42.11	88.22	0.000	0.5077
SUTA	66	east	8	–	–93.49	190.99	21.168	0.0000

105	west	4	–	–119.44	242.87	3.069	0.0855

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